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Abstract: Aim To determine the effects of competition and divergence time on morphological dissimilarity and geographical range overlap between dasyurid species at both regional and local scales. Our hypothesis is that speciation in this group has been largely allopatric at regional scale, but involved morphological divergence at local scale through sympatric character displacement. Location Australia, New Guinea and surrounding islands. Taxon Dasyurid (Dasyuridae) marsupials, 67 species. Methods Geographical range overlap was quantified using polygons representing the outer limits of species distributions. Local-scale range overlap was quantified as the degree of co-occurrence of two taxa across a set of ecological survey plots representing 83 sampled communities. Phylogenies were generated using a novel DNA dataset, with divergence times estimated via total-evidence dating incorporating fossils. Morphological divergence was determined using body mass and lower molar row length as proxy traits for reconstructing niche exploitation. Results Sister species pairs were found to be sympatric in 52% (11/21) of cases. Range overlap tended to increase with node age, which supports the hypothesis that mammalian speciation is routinely allopatric. We detected no evidence of character displacement with increasing range overlap between sister species pairs. However, a negative relationship was observed between morphological divergence in body mass and range overlap across all sampled taxa, suggesting that selection in sympatry is convergent, while divergent selection occurs in allopatry. Local-scale co-occurrences revealed no trace of species aversion, indicating that competition has not impacted on the spatial distribution of dasyurids. Main conclusions Despite moderate levels of sympatry through time, our results evince low rates of spatial co-occurrence between dasyurid species. Although this may be indicative competitive exclusion, the lack of character displacement suggests that biotic interactions have likely not acted as a dominant driver of phenotypic evolution in this radiation. We alternatively posit that abiotic factors including aridity and geographical connectivity have more feasibly propagated character convergence, and led to both niche conservatism and speciation in this ubiquitous australidelphian clade.

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The geography of speciation in dasyurid marsupials

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Abstract

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Keywords: age-range correlation; allopatric speciation; Australia; community phylogenetics; Dasyuridae; sister species

1. INTRODUCTION

Explaining patterns of species co-occurrence in relation to their ecological and morphological characteristics constitutes a core goal in many ecological investigations. Indeed, over the last 15 years, the incorporation of phylogenetic data into classic ecological studies on species coexistence has contributed to illuminate the processes underlying biotic assembly at different levels (from a local to a regional perspective) (reviewed in Warren et al., 2014). In this sense, two distinct approaches have been commonly employed, each one of them focused on a different spatial scale. On one hand, site-based approaches quantify spatial variation as the relatedness between co-occurring taxa and include measures of community phylogenetic structure and phylogenetic diversity (Webb et al., 2002; Vamosi et al., 2009). These methods - grouped into the field of community phylogenetics- are normally used to determine the role of ecological mechanisms (e.g., competition or environmental filtering) in structuring communities (Cavender-Bares et al., 2009; Cantalapiedra et al., 2014). On the other hand, regional scale analyses compare spatial distribution at deeper clade levels, and can thus reveal broader drivers of geographical speciation by quantifying the extent of range overlap between sister lineages (Anacker & Strauss, 2014; Hodgel & Bellwood, 2016; Gaboriau et al., 2018). Although local and regional scale analyses should ideally be applied in tandem to mitigate the influence of historical biogeography on currently extant species distributions (Mouquet et al., 2012; Wiens, 2012), only a few studies have evaluated such interlinked ecological and evolutionary perspectives simultaneously (Borregaard et al., 2014; Weeks et al., 2016). This paucity of studies addressing simultaneously the roles of history and ecology in biotic assembly is noteworthy as it is fairly clear that speciation history can impinge on community patterns at local scales (Cardillo, 2012), and likewise, there is evidence for the imprint of competition on broad-scale assemblage structure (Cardillo, 2011). Hence, although species with minimal regional overlap will usually exhibit limited co-occurrence at community level, the converse does not have to be necessarily true as fine-scale mechanisms (e.g., competitive exclusion) could prevent the coexistence of two species even when they show overlapping distributions. Consequently, under certain circumstances a high degree of range overlap may not translate into

97 real coexistence at a local scale. That is, in many cases sympatric species (in terms of broad-
98 scale spatial overlap) are not syntopic and do not interact ecologically (Cardillo & Warren,
99 2016).

100 Here, we assess the patterns of local and regional scale species co-occurrence within
101 Dasyuridae, a radiation of small-medium-sized carnivorous marsupials that incorporate some 75
102 named species (van Dyck & Strahan, 2008). Dasyurids are distributed across virtually every
103 terrestrial environment throughout Australasia, ranging from the Central Australian arid zone to
104 tropical rainforests in northeastern Australia and New Guinea (Dickman, 2003). The Dasyuridae
105 constitute a geologically recent radiation, which originated around the Palaeogene-Neogene
106 boundary (approximately 23 Ma), but diverged into its major crown groupings across the Mid-
107 Miocene Climatic Optimum (beginning around 18 Ma); this coincides with the tectonic
108 connection of Australia with New Guinea and the onset of cooler, dryer climatic conditions that
109 propagated more open habitats and intracontinental aridity (Krajewski et al., 2000; Westerman
110 et al., 2016; Kealy and Beck, 2017). These landmark events undoubtedly created novel
111 ecological niches, probably as result of the decline of competitors (e.g., thylacinids or
112 'marsupial wolves', and peramelemorphians, also known as bandicoots), and/or the emergence
113 of new habitats that promoted dispersal and vicariance processes (Morton et al., 1989). As result
114 of the vicariance speciation events, many extant dasyurid species today occur in only a narrow
115 range of habitat types, or over restricted geographical distributions and show allopatric
116 distributions. For example, the widespread xeric-adapted Dunnart, *Sminthopsis crassicaudata*, is
117 usually associated with cracking clay soils, whereas its close relative *Sminthopsis douglasi* is
118 limited to alluvial plain Mitchell grass pastures in central-northern Queensland (Woolley, 1992).
119 Likewise, spinifex (*Triodia*) grasses have been integral to the radiation of many arid-zone
120 dasyurid lineages (Anderson et al., 2019), including the tiny rodent-like Ningauis (*Ningaui*),
121 which primarily inhabit spinifex hummocks (Dickman, 2003).

122 Although they are widely distributed the continent and can be found in a wide range of
123 habitats, dasyurids exhibit a marked lack of morphological specialization compared to other
124 australidelphian marsupials (van Dyck & Strahan, 2008). Dasyurid marsupials show a

125 constrained basic body-plan and, apparently, morphological diversification has mostly involved
126 changes in body size (from mouse-like to dog-sized species), seemingly related with dietary
127 preferences: most dasyurids are insectivorous, except for the Mulgara (*Dasycercus cristicauda*),
128 Kowari (*Dasyuroides byrnei*), largest (>500 g) quolls (*Dasyurus*), and the Tasmanian devil, all
129 of which feed upon vertebrates (Fisher & Dickman, 1993). The lack of feeding niche
130 segregation amongst dasyurids suggests that the partitioning of food resource appears to occur
131 on prey size alone, which would accentuate the associated effect on body size differences (Fox,
132 1982). In this regard, Jones (1997) found evidence for competitive character displacement in
133 body size (measured as skull length) within the guild of dasyurid carnivores inhabiting
134 Tasmania (see also Jones & Barmuta, 1998). Subtler morphological and behavioural differences
135 appear to be common amongst sympatric species of the smaller-bodied insectivorous lineages
136 (Dickman, 1984). For example, the long-tailed (*Planigale ingrami*), and narrow-nosed
137 (*Planigale tenuirostris*) planigales, which maintain overlapping distributional ranges, can be
138 distinguished by relative flattening of the cranium (Archer, 1976). Intraspecific competition has
139 also been evoked for explaining why the agile antechinus (*Antechinus agilis*), a scansorial
140 species, spend more time foraging on the ground once the sympatric and fossorial Swainson's
141 antechinus (*A. swainsonii*) is removed from its range (Dickman, 1986a,b). A similar
142 phenomenon has been proposed (Dickman, 1988) to explain the delayed breeding schedule of *A.*
143 *agilis* in comparison to its co-occurring relative, the brown or Stuart's antechinus (*A. stuartii*).
144 Noticeably, the strength of competition appears to be greater in mesic environments that
145 sustain high population densities (forests, heathlands) but where the number of co-occurring
146 species is low (2-3 spp.) in comparison with xeric habitats, where the unpredictability of food
147 resources maintains population densities at low levels, thereby decreasing the probability of
148 interspecific encounters (Dickman, 2003). Despite the extreme climatic conditions (variable
149 rainfall, severe drought) to which organisms present in arid and semi-arid environments must
150 face, up to 9 dasyurid species can co-exist in this region. The unexpected high dasyurid
151 diversity present in harsh environments (deserts, hummock grasslands) characteristics of the
152 Australian arid zone has been associated to the existence of increased cladogenesis in this region

153 in several taxonomic groups including the Dasyuridae (e.g., Rabosky et al., 2007; Catullo &
154 Keogh, 2014; García-Navas et al., 2018). At a local scale, lack of pressure from competition
155 may also have contributed to maintain high species richness in this region (Crowther & Blacket,
156 2003). Alternatively, such patterns may arise as result of the existence of substantial niche
157 partitioning based on body size (i.e., small body size overlap) in agreement with the limiting
158 similarity principle (MacArthur & Levins, 1967; Grant & Grant, 2006).
159 In this study, we examine the relationship between species co-occurrence patterns and
160 morphological similarity in dasyurids at both regional and local (community) scales. Our
161 hypothesis is that speciation in this group has been largely allopatric at regional scale, as
162 previously shown in other taxonomic groups (Fitzpatrick & Turelli, 2006), and that in those
163 cases where sympatry exists, it involves morphological divergence at local scale through
164 character displacement (e.g., Grossenbacher & Whittall, 2011). Although interspecific
165 competition should favor diversification of functional traits, competition for resources may also
166 lead to adaptive convergence whether the benefits to an individual of excluding heterospecifics
167 from their territory are similar to the benefits of excluding conspecifics (Cody, 1969; Drury et
168 al., 2018). This is especially pertinent for harsh xeric environments where density-dependent
169 factors are important, and selection may favor trait convergence (e.g., body mass) to establish
170 dominance hierarchies and mediate territorial interactions (e.g., Fox, 1982). Thus, we controlled
171 for similarity in habitat when testing whether interspecific competition leads to morphological
172 convergence. Next, we used community data to address the relationship between local scale
173 species co-occurrence and morphological divergence and test whether those species that co-
174 exist in the same assemblages (positive associations) are more morphologically divergent that
175 those that do not coexist (negative associations) or do so not preferentially (random
176 associations). Lastly, we used a novel approach, node-based analysis (Borregaard et al., 2014),
177 to quantify the distributional divergence between daughter lineages descending from the same
178 node and thereby obtaining a better understanding of the phylogenetic structure of species
179 assemblages. Since the four tribes conforming this family share a complex biogeographic

history of dispersals across Australia and Papua New Guinea (García-Navas et al., 2018), we expect a low number of nodes to exhibit strong distributional change.

2. MATERIAL AND METHODS

2.1 Phylogeny and sister species pair selection

We first derived a novel phylogeny of Dasyuridae using a modified version of the total-group Dasyuromorphia DNA sequence dataset compiled by Westerman *et al*. (2016). This 17,968 bp matrix included an expanded ingroup sample of 80 extant dasyurid taxa (see Fig. 1), together with nDNA sequence data for the omega globin, runt-related transcription factor 2 (*RUNX2*), and *col2A1* enhancer genes (see Supplementary Data). Corresponding information was also transcribed from the recently published outgroup thylacine (*Thylacinus cynocephalus*) genome (Feigin et al., 2018). We then ran a subset analysis that pruned the ingroup dasyurid taxon sample (primarily via deletion of closely related terminals within the *Antechinus* species complex) to match the 67 extant species represented by our ecomorphological data. A phylogenetic divergence timescale was estimated using node + tip total evidence dating following Kealy & Beck (2017). We augmented their 115 craniodental/postcranial skeletal character dataset with five new fossil taxa to test alternative node calibrations (total taxon sample = 100), but otherwise retained the original parameters and settings. Further details about our phylogenetic and tree dating analyses are provided in the Supplementary Material.

Twenty-one sister species pairs (= most closely related sister taxa) were identified from our time-calibrated total evidence tree based on >0.95 posterior probability (PP) support at their most recently divergent node (see Supplementary Material). Because the majority of taxa not included in our analysis belonged to the same *Antechinus* species complex, we deemed their omission to have minimal impact on our overall hypothesis of dasyurid interspecific relationships. Pairwise divergence times were then calculated using the 'chronoMPL' function in the *ape* library (Paradis et al., 2004).

208 *2.2. Character selection and divergence estimation*

209 We gathered data on overall body size (expressed as both body mass and maximum snout-tail
210 length) and length of the lower molar row (m_1-m_4) for a sample set of 67 dasyurid species
211 (accounting for 89% of the total clade species count) based on information available in the
212 published literature (Table S1; Supplementary Data). Overall body size, which ranges from 52
213 mm and 11.6 g in *Ningaui yvonneae* to 611 mm and 8,000 g in *Sarcophilus harrisii*, constitutes
214 a key attribute for any organism determining ecological interactions (e.g., who eats whom and at
215 what rate) and confers fitness advantages in form of size-dependent competition for resources,
216 increased fecundity and greater diet breadth (e.g., Kraaijeveld-Smit et al. 2003; Fisher &
217 Cockburn, 2006). As an example, Dickman (2014) reported a positive relationship between
218 body mass and percentage intake of vertebrates in the diet of 25 dasyurid species. Dental
219 morphology is also generally indicative of diet (e.g., Pineda-Munoz et al., 2017; Martin et al.,
220 2016), and while dasyurids lack specialized carnassials, their four pairs of molars are massive
221 and structurally comparable between species (Archer, 1976; 1978). Because overall body and
222 tooth size can be correlated in marsupials (Gordon, 2003), the length of the lower molars was
223 corrected for body size using a least squares regression analysis. The resulting residuals were
224 used as input in further analyses. As body size and body mass are highly correlated ($r = 0.85$, p
225 <0.001) and we obtained similar results, for the sake of brevity we only report the results of our
226 body mass analyses here.

227 We used sister species pair comparisons to evaluate the relationship between
228 morphological disparity in overall body size and molar row length against patterns of regional
229 co-occurrence. Character divergences were quantified following the approaches of Davies et al.
230 (2007) and Anacker & Strauss (2014), which contrast the logarithm of trait values between
231 sister-pairs in the form of: $log\ (X_A) - log\ (X_B)$ where X was the trait value and $X_A > X_B$.

232

233 *2.3 Range overlap estimation*

234 To quantify range overlap between species pairs, we converted species' distribution maps
235 retrieved from the IUCN website (IUCN, 2018) to vector polygons. These were collated with

official biodiversity records from the Atlas of Living Australia (http://www.ala.org.au), and rasterized to a 100×100 km grid using ArcGIS to obtain a presence-absence matrix. This dataset was used to compute the level of range overlap between species pairs using the R package *letsR* (Vilela & Villalobos, 2015). Range overlap represents the proportion of co-occurrence affecting each species within the combined range of each pair of species (Chesser & Zink, 1994; Martin et al., 2010); this is expressed as a value between 0 (no overlap) and 1 (individual species range completely overlapped by the larger range). We accordingly classified our 21 sister species pairs as being either allopatric (no overlap), or sympatric (overlap), and examined the variation in range overlap relative to divergence time and degree of morphological dissimilarity (evidenced by contrasting phenotypic traits) using univariate regression models. To test the robustness of our results against models of trait evolution (Brownian motion: Felsenstein, 1985), we repeated these regressions with correction for divergence time by dividing the observed overlap with the square root of the sum of the branch lengths connecting the species pairs (*sensu* Davies et al. 2007). In addition, we assessed morphological dissimilarity between allopatric and sympatric pairs of sister species by applying *t*-tests.

2.4 Geography of speciation

We examined how range overlap varies with divergence time using an 'age-range correlation' (ARC) test to yield information about the geography of speciation (see Fitzpatrick & Turelli, 2006). Intercept values ≥ 0.5 and a negative slope were treated as indicative of predominantly sympatric speciation, whereas intercepts ≤ 0.5 and positive slopes are suggestive of allopatric speciation (Fitzpatrick & Turelli, 2006).

2.5 Testing for sympatric convergence

We created a dissimilarity index by calculating the square-root transformed Euclidean phenotypic distance based on differences in terms of body mass and molar row length between all pairs of species. This was then correlated with our pairwise matrix of range overlap using a Mantel test to establish whether sympatry is negatively associated with dissimilarity, as would

be expected if trait convergence arises as consequence of interspecific interactions. Because convergence in sympatry can also result from selection favoring particular phenotypes from comparable environments, we accommodated for habitat by using generalized categorizations: 1. forests; 2. woodlands, heathlands and mallee; and 3. grasslands and sand-plains. If, after controlling for compatibility in environmental conditions, sympatry is negatively correlated with the morphological dissimilarity index, then this would support the inferred existence of trait convergence as result of interspecific interactions. We used partial Mantel tests to examine the relationship between spatial overlap and morphological divergence controlling for phylogenetic distance. Patristic distances were computed using *adephylo* (Jombart et al., 2010). Mantel tests were implemented in R using the *vegan* package (Oksanen, 2010).

2.6 Local scale species co-occurrence

To assess whether our observed regional scale patterns are thus informative of processes operating at local scales (e.g., ecological interactions), we quantified local-scale co-occurrences between Australian species. We compiled occurrence data for a total of 83 local communities from scientific articles, book chapters, and supplements of the Western Australian Museum (see Supplementary References for full literature list). We then tested for statistically significant pairwise patterns of species co-occurrence by applying the approach proposed by Veech (2013) to our community data-based presence-absence matrix. Thereby, we determined the probability that any pair of species would co-occur at a frequency greater or lesser than the observed frequency if the two given species are distributed randomly (independently) of one another. We only considered those species pairs that co-occurred across a minimum number of plot surveys, and yielded frequencies >1. We then tested for differences in the level of morphological similarity between those species that positively co-occurred, and those that showed a negative or random association.

In addition, we quantified the degree of co-occurrence among all pairs of species across our local dataset (i.e., Australian taxa that were recorded in at least one survey plot) *via* their *c*-scores (= checkerboard score: Stone & Roberts, 1990). High *c*-scores indicate reduced instances

292 of co-occurrence, and suggest the influence of mechanisms such as competitive exclusion.
293 Potential relationships between local and regional scale co-occurrences (measured as degree of
294 range overlap and *c*-scores, respectively), phylogenetic distance, and level of morphological
295 dissimilarity in sympatric species were further assessed using Mantel tests with non-overlapping
296 species pairs excluded. These analyses were implemented using the R packages *cooccur*
297 (Griffith et al., 2016) and *picante* (Kembel et al., 2010).
298
299 *2.7 Node-based analysis*
300 We used the node-based method of Borregaard et al. (2014) to combine ecological and
301 evolutionary patterns into a single framework; this samples each node in a given phylogeny and
302 compares the distribution of descendant clades in our phylogeny against a null model. The
303 resulting 'specific overrepresentation score' (SOS) provides a measure of clade
304 overrepresentation that integrates both clade-based and site-based approaches. SOS values
305 calculated for a certain node can be summarized across occupied sites to yield the 'geographic
306 node divergence' (GND), which quantifies the distributional divergence between the two
307 daughter lineages descended from a given node. GND thus identifies which nodes are
308 responsible for observed patterns of phylogenetic structure and regional scale species co-
309 occurrence (see Supplementary Material for details).
310
311
312 3. RESULTS
313 *3.1 Phylogenetic and tree dating inferences*
314 Our analysis of the expanded DNA sequence phylogenetic dataset yielded an almost identical
315 tree topology (Fig. S1) to that produced by Westerman et al. (2016). All nodes comprising the
316 extant ingroup dasyurid clades retrieved virtually unanimous support (PP = 0.98–1), except for
317 placement of the dunnart species *Sminthopsis granulipes* (PP = 0.77), and *Sminthopsis*
318 *youngsoni* + *Sminthopsis hirtipes* (PP = 0.61) within Sminthopsini, and the planigales *Planigale*

319 *maculata* + *Planigale novaeguineae* + *Planigale ingrami* + *Planigale gilesi* (PP = 0.57), and *P.*
320 *ingrami* + *P. gilesi* (PP = 0.7) within Planigalini (compare with Westerman et al., 2017).
321 Our total evidence node + tip dated tree topology (Fig. 1) generated dasyurid crown
322 clade divergence estimates (Table S2) that are generally younger than those advocated by other
323 studies (Westerman et al., 2016; Kealy & Beck, 2017). Most significantly, the initial radiation
324 of extant dasyurid lineages was reconstructed as coinciding with the Mid-Miocene Climatic
325 Optimum (around 15 Ma), a result that post-dates other estimates by up to 5 Ma (see Kealy &
326 Beck, 2017). Cladogenic events propagating the extant dasyurid species-level lineages thus
327 accompany the onset of aridity during the late Miocene and Pliocene (commencing from about
328 10 Ma). However, we emphasize that divergence times within Dasyuromorphia are sensitive to
329 a priori dataset selection and preferred parameters, with DNA-only analyses consistently
330 yielding substantially older node ages (see discussion in Kealy & Beck, 2017); this concurs with
331 the contrasting time-trees generated for other australidelphian marsupial clades (e.g., Kear et al.,
332 2016; Travouillon & Philips, 2018).
333
334 *3.2 Sister species analyses*
335 We detected no statistically significant differences in average node age and divergence in terms
336 of body mass or molar row length between sympatric and allopatric sister species pairs within
337 Dasyuridae (*t*-tests, all *p*-values > 0.1; see Table S3). The degree of range overlap between these
338 same species pairs was also not correlated with the level of morphological divergence regardless
339 of which trait was analyzed (body mass: $F = 0.16$, $p = 0.70$; molar row length: $F = 0.01$, $p =$
340 0.92). We obtained similar results when repeating the regression models controlling for
341 divergence time (both *p*-values >0.5). There was likewise no significant linear relationship
342 between divergence time and either body mass ($F = 0.38$, $p = 0.25$) or molar row length ($F =$
343 0.11, $p = 0.74$), even when analyzing sympatric and allopatric pairs separately (all *p*-values
344 >0.05).
345
346 *3.3 Age-range correlation test*

347 Range overlap tends to increase with time since divergence (node age), although this
348 relationship was not statistically significant (slope = 0.07, intercept = 12.47, $F = 1.39$, $p = 0.25$).
349 This result was also consistent (slope = 0.06, intercept = 10.51, $F = 1.25$, $p = 0.28$) after
350 excluding sister species pairs with PP values <1 (Fig. 1).
351
352 *3.4 Range overlap and morphological dissimilarity*
353 We found no significant relationship between the level of sympatry (range overlap; average
354 value = 11.8%) and morphological distance between species pairs (Mantel test, $p = 0.11$).
355 However, pairwise dissimilarity in body mass was negatively correlated with the degree of
356 range overlap (Mantel test, $r = 0.06$, $p = 0.015$: Fig. 2) when examined on its own; this suggests
357 that species more similar in terms of body mass overlap more in their geographical range. When
358 grouped by habitat type, a relationship close to being significant was also identified for species
359 living in grasslands and sandplains ($n = 17$ spp., $r = 0.18$, $p = 0.071$), whereas more productive
360 woodland ($n = 26$ spp., $p = 0.18$) and rainforest ($n = 15$ spp., $p = 0.94$) environments returned no
361 significant relationship. The correlation between body mass dissimilarity and range overlap
362 became statistically non-significant when controlling for phylogenetic distance (partial Mantel
363 test, $p = 0.13$). Range overlap and dissimilarity in molar row length was also not significantly
364 related (Mantel test, $p = 0.62$).
365
366 *3.5 Local scale species co-occurrence analyses*
367 Forty-one of the 55 named extant Australian dasyurid species were recorded at least once in the
368 83 local survey plots included in this study, with the antechinus *Antechinus stuartii*, and
369 dunnarts *Sminthopsis crassicaudata* and *Sminthopsis dolichura* being represented in 24%, 23%,
370 and 18% of the total sample set, respectively. Overall species richness (α-diversity) was low at
371 most sites (average = 3.1 spp.), but this may reflect sampling biases resulting from more
372 frequent documentation of mesic temperate regions in Western Australia, New South Wales,
373 and Victoria. Conversely, the arid areas of South and Central Australia, and the tropical belt of
374 northern Australia were under-represented, and it likely explains the conspicuous absence of the

375 desert-adapted mulgara, *Dasycercus blythi*, and tropical savannah inhabitants such as *Planigale*
376 *ingrami*, from our dataset (Fig. 3). Absence of the Kakadu dunnart (*Sminthopsis bindi*), and near
377 threatened Carpentarian pseudantechinus (*Pseudantechinus mimulus*) probably evidence their
378 extremely restricted geographic distributions.

379 Of the 100 species spairs assessed using the methodology of Veech (2013), 22 showed
380 significant levels of attraction, while only seven exhibited aversion (Table S4). Only one of the
381 seven aversive (i.e., 'checkerboard') species pairs involved species with overlapping ranges: the
382 antechinus *Antechinus flavipes*, and dunnart *S. crassicaudata*). All other pairs were allopatric
383 species, specifically, these involved *A. stuartii* (endemic to eastern Australia, from southern
384 Queensland to southern New South Wales) and the otherwise broadly distributed species of
385 *Sminthopsis* and *Ningaui* (Fig. S2). Species pairs that showed a significant attraction were also
386 not more morphologically divergent in body mass or molar row length compared with those
387 expressing random or significant aversion (body mass: $t = 0.21$, $p = 0.83$; molar row length: $t = -$
388 0.23, $p = 0.82$).

389 Lastly, we detected no meaningful association between the co-occurrence metric and
390 extent of range overlap (Mantel test, p = 0.40: Fig. S3), or morphological dissimilarity (Mantel
391 test, p = 0.93) when all geographically overlapping species pairs were examined. This result was
392 consistent when body mass and molar row length were analyzed separately (all p-values >0.05).
393 Nevertheless, the levels of co-occurrence did decrease with phylogenetic distance (Mantel test, r
394 $= 0.07$, $p = 0.01$).

395

396 *3.6 Node-based analysis*

397 Only one node (marked "A" in Fig. 1) within our total evidence node + tip dated tree exhibited a
398 high degree of allopatry (GND score >0.65), indicating distributional segregation amongst its
399 descendent lineages. This corresponds to the late Miocene split (about 7.8 Ma) between the
400 Australian wambengers (*Phascogale*) and New Guinean murexias (*Murexia*). Most other nodes
401 with high GND scores were dispersed throughout the basal divergences in our topology, and
402 constitute major clade subdivisions within Dasyuridae.

403

404

405 # 4. DISCUSSION

406 ## *4.1 Sister species comparisons: testing for character displacement*

407 The level of sympatry (52%) observed in our sample of dasyurid sister species pairs was slightly
408 higher than that generally reported amongst placental mammals (33-45%: Fitzpatrick & Turelli,
409 2006). Our analysis of range overlap and trait divergence showed no evidence that competition
410 reduces geographic range overlap in species with similar body sizes, or conversely, that range
411 overlap promotes body size divergence. This lack of competitive displacement might be
412 byproduct of climatic niche conservatism, which clearly affects climatic tolerances within
413 Sminthopsini -one of the most speciose arid-adapted dasyurid clades- (García-Navas &
414 Westerman, 2018). However, when testing if sister species were more similar to each other in
415 terms of body mass and dentition with respect to other non-sister congeners, we found that it
416 was true for roughly one quarter of cases (25% for body mass; 31% for molar row length). At
417 this point, two important factors must be considered when interpreting these results. First, the
418 existence of geographic range overlap does not guarantee co-occurrences at local scale. As our
419 data shows (Table S3), species can distribute micro-allopatrically within local scale
420 communities despite manifesting regional scale sympatry. This minimizes the need for
421 competition-driven trait divergence, and could thus explain the lack of a relationship between
422 regional range overlap and morphological divergence, as well as between range overlap and *c*-
423 scores. Second, our estimates may average over remarkable intraspecific variability; despite a
424 lack of difference in species-wide mean values, populations in close proximity may exhibit
425 character displacement (Anacker & Strauss, 2014).

426

427 ## *4.2 The geography of speciation*

428 When plotting range overlap against node age for our 21 identified sister species pairs, we found
429 that allopatry potentially played a more impactful role than sympatry in dasyurid speciation
430 processes. This concurs with the established observation that smaller-bodied mammals

(including gophers, kangaroo rats, pocket mice and shrews among others) tend to undergo allopatric speciation (Fitzpatrick & Turelli, 2006); however, our results were not significantly supported (even following exclusion of *Murexia naso* + *Murexia melanurus*: slope = 0.11, intercept = -3.68, $F = 3.47$, $p = 0.07$; Fig. S4), probably because of small sample size. Here, we restricted our analyses to recent speciation events with differing relative divergence times (i.e., sister species comparisons) in order to mitigate some concerns regarding the lability and dynamic nature of species distributions (see e.g. Losos & Glor, 2003; Skeels & Cardillo, 2019). Such phenomena can manifest as trait divergences expressed across overlapping regions in the past, but subsequently exhibit minimal range overlap because of shifting ranges over time (evidenced *via* equivocal speciation history models: Fitzpatrick & Turelli, 2006). Conversely, recent simulations suggest that speciation history can produce detectable distributional and phylogenetic signals, even when species ranges have evolved substantially (Skeels & Cardillo, 2019). Accordingly, our results show that even in families in which species are highly mobile (see e.g., McLean et al., 2019) and there is a moderate proportion (>50%) of sympatric sisters, it is possible to find a subtle signature of allopatric speciation (positive ARC) supporting the view that sympatric speciation in usually rare among vertebrates (Phillimore et al., 2008).

4.3 *Range overlap and morphological divergence*

We failed to find a significant relationship between range overlap and morphological distance in dasyurid species, which indicates that biotic interactions have not played an important role in determining the spatial distribution of dasyurid species. Also, we did not find a relationship between the level of range overlap and dissimilarity in molar row length. This is in contrast with that reported by Davies et al. (2007) in a study across carnivores. Davies and colleagues found that species that differ more in carnassial tooth length overlap more in their geographical range. They also concluded that interspecific competition for food is a critical factor determining species co-existence in carnivores as upper carnassial length was better predictor of geographical range overlap than either canines or body size (Davies et al., 2007). However, they did not conduct analyses within each family due to small sample size and, in fact, two out of the

seven families analysed -Herpestidae and Procyonidae- did not show a positive trend between range overlap and divergence in carnassial length, which suggests that the reported trend seems not to be widespread within mammal families. Dasyurids lack specialized carnassials since they are mostly insectivorous and their diet includes a low proportion of vertebrates which largely varies among species (Dickman, 2014). Consequently, dental morphology is probably not subject to strong selection in this family of microcarnivorous

With regard to body mass, we found a negative relationship between this trait and range overlap (Fig. S5), implying that convergent selection has occurred in sympatry, while divergent selection has occurred in allopatry (i.e., abiotic factors are dominant). However, when cross-referenced against habitat, we only recovered a close-to-significant relationship for those species living in grasslands and sandplains, suggesting that such hostile environments likely promote character convergence. Notably, this concurs with previous studies of desert mammal communities, which tend to yield high species diversity relative to body size (see Shenbrot *et al*., 1999 for a review). Co-existence between species of different body sizes has been attributed to competitive exclusion (Brown & Nicoletto, 1991), size-related niche segregation affecting preferred food resources (Brown & Lieberman, 1973; Alhajeri & Steppan, 2018), and/or contrasting spatial distributions (vis-à-vis dispersed *versus* grouped food resources: e.g., Hutto, 1978). In contrast, Australian arid zone dasyurid communities (which support up to eight–nine species) exhibit an opposing trend -convergent body size- that may be influenced by two complementary factors. Firstly, strong selection for an optimal body size that accommodates for both thermoregulatory (e.g., body size reduction as an advantage for harsh climates) and dispersive requirements (e.g., body size increase facilitating migration to utilize widely distributed food resources) in harsh environments. Secondly, reduced probability of interspecific encounters because of low population densities (a product of unpredictable food supplies) and/or strong micro-habitat selection. Overall, our results thus support the hypothesis that competition exerts only minimal constraint on regional scale species coexistence within Dasyuridae (Dickman, 2003).

487 *4.4 Local scale species co-occurrence analyses*

488 At local scale, we found no evidence that competition has determined spatial distribution
489 between species within dasyurid local communities. Indeed, within our sampled survey plots the
490 number of species pairs showing attraction was significantly greater than the number evincing
491 aversion. Our results are therefore inconsistent with what would be expected according to the
492 competitive exclusion hypothesis (i.e., a prevalence of negative interactions; Connor &
493 Simberloff, 1979), and supports the null hypothesis that dasyurid species co-occurrence is
494 random at population level. Furthermore, we tested whether the likelihood that the distribution
495 of one species has been directly affected by the presence of other species increased as the degree
496 of range overlap increases. Interestingly, we discovered that species with substantial overlap
497 tended to have lower *c*-scores (i.e., higher randomness), although this relationship was not
498 statistically significant. It suggests that niche-based processes (competition) have a negligible
499 impact on dasyurid distributions. Co-occurrence data also revealed that dasyurid assemblages do
500 not exhibit close packing. Consequently, sister species pairs were usually uncommon in local
501 communities with less than half of the sympatric sister species pairs being recorded in the same
502 survey plot (Table S3). Lastly, we didn't find a relationship between morphological divergence
503 and co-occurrence at a local scale, which reinforce findings obtained at the regional scale (see
504 above); biotic interactions don't seem to play an important role in shaping the distribution
505 ranges composition of dasyurid assemblages.

506

507 *4.5 Node-based analysis*

508 Lastly, our node-based analysis pinpointed only a single node exhibiting strong distributional
509 change (geographic node divergence GND score >0.65). This corresponds to the marked
510 distributional segregation between the Australian *Phascogale* and New Guinean *Murexia*. The
511 otherwise universally low GND scores calculated for other clades within Dasyuridae (indicating
512 a dearth of geographically differentiated lineages in Australia *versus* New Guinea) concurs with
513 the recognised biogeographical ubiquity of the group, and the hypothesis that colonization of

514 novel New Guinean habitats probably occurred opportunistically via multiple waves of
515 migration commencing in the later Neogene (García-Navas et al., 2018).
516
517 *4.6 Conclusions*
518 Overall our results highlight the analytical advantages of examining species overlap at different
519 spatial resolutions (Cardillo & Warren, 2016). Moreover, by integrating approaches used to
520 infer broad-scale, evolutionary processes (phylogenetic comparative methods) and those
521 commonly used to study ecological interactions at fine scales (community ecology), we show
522 that it is possible to obtain a comprehensive understanding of factors driving species
523 distributions. Specifically, we posit that geographic isolation arising from niche conservatism
524 (as opposed to biotic interactions including competitive exclusion) has played a pivotal role in
525 shaping the speciation patterns, and led to one of the most widespread endemic mammal
526 radiations found on the Australasian landmasses today (García-Navas & Westerman, 2018).
527
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533
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Biosketch

721 **Vicente García-Navas** is a postdoctoral fellow at the University of Zurich in Switzerland. His
722 research focuses on the macroevolutionary implications of geographic diversity concentrations
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726 australidelphian marsupials.
727 **Michael Westerman** is an Adjunct Professor at La Trobe University in Australia, and a leading
728 specialist on the genetics and molecular systematics of Australasian mammals.
729
730 *Author contributions*
731 V.G.N. designed the study; V.G.N and M.W. compiled the ecomorphological data; M.W. and
732 B.P.K. compiled the phylogenetic data and analyses; V.G.N carried out the analyses and wrote
733 the manuscript with input from B.P.K. and M.W. All authors read and approved the final
734 manuscript.
735
736 *Data availability statement*
737 The data supporting the results are available from the LabArchives Repository:
738 XXXXXXXXXXXXXX
739 Title: Data from: The geography of speciation in dasyurid marsupials
740 DOI: XXXXXXXXXXXX
741 Journal: Journal of Biogeography
742 Journal manuscript number: JBI-19-XXXX
743

744 *Figure captions*

745

746 **Fig. 1.** Time-calibrated maximum clade credibility tree of crown Dasyuridae. Blue and red
747 branches represent sympatric and allopatric sister species, respectively. Sister species pairs with
748 posterior probability < 1 are indicated with an asterisk. Gradient scale (top right) and node
749 symbol diameter (coloured circles) are proportional to GND at each node (see main text). Only
750 fully resolved nodes where both descendant clades consist of at least two species were included
751 in the node-based analysis. Distributional maps ("A-C") represent SOS values for the
752 corresponding nodes ("A-C") with high GND scores; highest GND score > 0.65 (arrow). Colour
753 gradient indicates over-representation of opposing descendant clades (red versus blue) *versus*
754 both descendant clades being equally represented (yellow).

755

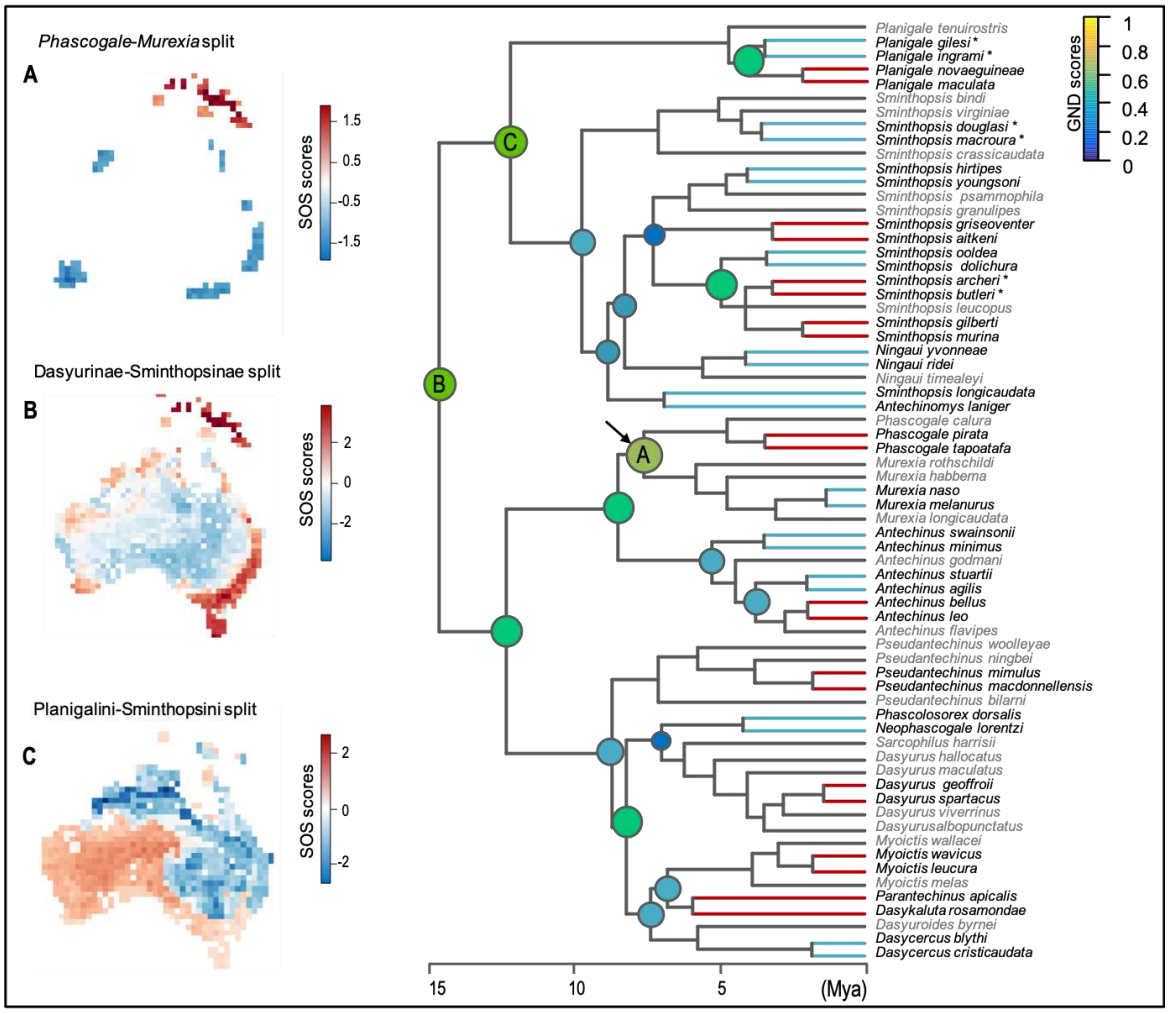
756 **Fig. 2.** Scatter plot of (transformed) range overlap against body mass divergence quantified as
757 morphological distance (square-root transformed Euclidean distance) based on pairwise
758 differences in body mass (Mantel test, $r = 0.06$, $p = 0.015$). In the x-axis, a value of zero means
759 complete overlap (i.e., complete sympatry), and a value of 1 would mean complete allopatry.
760 Both sympatric and allopatric pairs of species are included. Exclusion of non-overlapping pairs
761 resulted in a steeper linear relationship (grey regression line; see Supplementary Material).
762 Artwork courtesy Kevin Stead.

763

764 **Fig. 3.** Map of Australia showing the approximate location of the 83 local survey plots
765 (representing small mammal communities) herein (see Supplementary Material). Pie charts
766 indicate the percentage of *n*-species communities in each region. Richer communities (>6
767 species) are located in the arid areas of Queensland, northeastern Australia. The map of the inset
768 shows the spatial distribution of species richness of dasyurid marsupials in the Australo-Papuan
769 region. The Australian arid zone is the region with the greatest species diversity (yellow-orange
770 areas) whereas some regions across the 'Top End', Northern Territory (empty cells), do not
771 harbor any dasyurid species.

776 Figure 1

777



778 Figure 2

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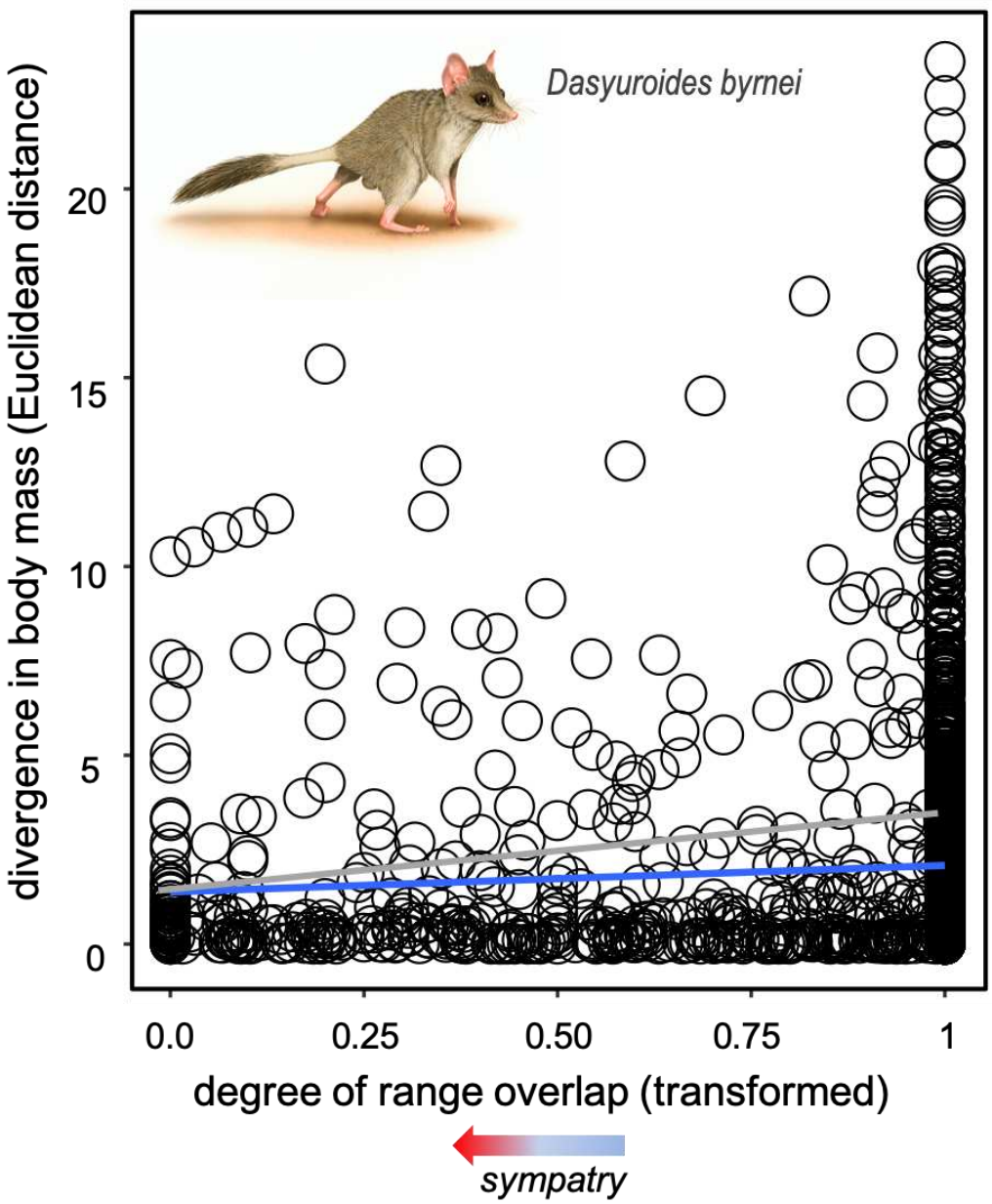

789 Figure 3

790